Out of Africa and into the Levant: replacement or admixture in Western Asia?

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Abstract

Late Pleistocene Israel is the region in which issues of population mixture or competition at the time of the emergence of modern humans are most likely to be solved. For those who believe that modern humans first arose in Africa and subsequently spread throughout the world replacing archaic populations, the Levant would be the first region where such archaic populations were encountered. For those who regard the Levantine Neandertal populations as late émigrés from a glaciated and inhospitable Europe, the Levant is the place where it is most likely that Neandertals encountered other human populations. If ever there was a time and place where we can examine the question of whether European and African populations exchanged ideas and mates, or competed with each other without genetic exchanges, this is it! In this paper we test the null hypothesis of a single human species occupying the Levant at the onset of the Late Pleistocene. An inability to delineate two distinct groups among the Levantine hominids would support the null hypothesis, while a demonstration of the presence of two morphs would lead to its refutation. We use non-metric traits to examine the eight most complete adult Levantine human crania to try to refute the contention first proposed by McCown and Keith (1939. The Stone Age of Mount Carmel: the Fossil Human Remains from the Levalloiso-Mousterian, Vol. II. Clarendon Press, Oxford), that the Levant "Neandertals" (Amud, Tabun) were the same species as the "early modern humans" (Qafzeh III, VI, IX; Skhul IV, V, IX). To test this hypothesis we use individual specimens as "operational taxonomic units", and assess it using phylogenetic analysis as a heuristic clustering procedure. While our analyses produce many different trees, none of the most parsimonious ones reveal a separate Neandertal clade. Furthermore, we conducted a pairwise difference analysis of these data, which also failed to reveal a unique relationship between the Neandertal crania that would be expected if these hominids were a different species from that represented by Qafzeh and Skhul. We acknowledge that the bases for refutation are necessary but not indispensably sufficient conditions, and yet nevertheless, our findings fail to refute the null hypothesis. Instead our results suggest that the traditional "Neandertal" versus "modern human" groupings in the Levant may not be as distinct as often thought. This would imply that as populations left Africa, they interbred with the Late Pleistocene inhabitants of the Levant, and suggest that as different populations moved or expanded their range, subsequent human evolution be viewed as a consequence of the continued mixing of ideas and genes. © 2001 Elsevier Science Ltd and INQUA. All rights reserved.

1. Introduction

While most hypotheses of a single recent origin for modern humans focus on Africa as the place of humanity's beginnings, it is the Levant where the first cranial samples attributed to the earliest modern humans can be found (Delson, 1988; Stringer, 1988, 1990; Bar-Yosef, 1992). This is a key region for understanding the role of Africa in modern human origins, because the issue revolves mainly on whether modern humans were a new species, and this can only be convincingly resolved with evidence of reproductive behavior when other putative species were encountered. By virtue of its place and date, the Levant has the earliest sample with relevant data.

Late Pleistocene human remains from western Asia are numerous, dated, and well described. The earliest large sample was from the Mount Carmel caves, and interpretations of its variation first raised the question of whether two distinct species, or two populations from the same evolving species, were represented (McCown and Keith, 1939; Dobzhansky, 1944; Thoma, 1962; Howells, 1973; Gould, 1988). An earlier description of the Mount

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Carmel remains from Skhul and Tabun (McCown and Keith, 1939) suggested the presence of only one type of human characterized by a wide range of variation. McCown and Keith were the last to view all of the Mount Carmel remains together. They concluded that the variability was due to the sampling of an evolving lineage, or the mixture of different geographic groups. They did not attribute it to the confusion of different human species. However, the Eve Theory requires that the sample be interpreted to show the mixture of different species, as modern humans emerged from Africa and encountered archaic populations, and Eve theorists have even suggested that the variation at Skhul itself reflects such a mixture (Tattersall and Schwartz, 1999). Yet, 60 yr later, we can still ask whether McCown and Keith can be shown to have been wrong, a logical prerequisite to accepting the Eve Theory, and whether the categories "Neandertal" and "early modern *Homo sapiens*" validly apply to the Levantine sample.

Therefore, the Levant provides the means for understanding the timing and mechanisms of the modern human occupation of the rest of the world, if modern humans originated in Africa as a distinct group. This is because it was in Western Asia that the putative earliest modern humans first encountered other hominid populations. These modern human populations were not restricted to Africa until they could *avoid* penetrating the Levant where they would have to encounter Neandertal populations (Cavalli-Sforza, 1998).[1] To the contrary, we might expect early modern humans in the Levant after they appeared in Africa, with features that could identify them both as modern and as African, and behaviors that could account for how they were able to replace the archaic populations they encountered.

The hominid remains from the Levantine sites of Skhul and Qafzeh are generally thought to represent these Africans, and are referred to as "anatomically modern humans". It is widely believed they are the earliest examples thereof. These facts are cited in support of various "Out of Africa" hypotheses. Skhul and Qafzeh have dates that are barely within the Late Pleistocene. Thermoluminescence dates for Skhul level B are 119 ± 18 kyr and for Qafzeh they range between 102 and 85 kyr (Valladas et al., 1998). Electron spin resonance dates for Skhul are 101 ± 13 (LU) and 81 ± 15 (EU), and for the Qafzeh burials 115 ± 15 (LU) and 96 ± 13 (EU), according to a recent review by Bar-Yosef (1998). These sites overlap in age with European Neandertals and may be earlier than the Levantine Neandertals (although this is

not absolutely clear, as the age of the Tabun female is uncertain; for instance compare Valladas et al. (1998) and Simpson et al. (1998)). Many authors now regard the Skhul and Qafzeh hominids as constituting a different species from the Levantine Neandertals (Rak, 1993, 1998; Tattersall, 1996; Lieberman, 1998a; Stringer, 1998). The identification of two penecontemporary human species in this region reflects the more general notion that Neandertals and modern humans are distinct biological species, a notion certainly supported by repetition, if not by fact. As Franciscus (1999, 1808) recently wrote: "there is today a greater tendency among paleoanthropologists to view Neandertals as a species distinct from *H. sapiens* … certainly not all specialists in this area concur, but those who do not are increasingly in the minority".

However, when the human remains from Mount Carmel were first described and systematically compared to other human fossils (McCown and Keith, 1939), the Skhul specimens were neither considered as a different species from the Tabun woman and the other Tabun remains, nor were they interpreted as "modern humans". The Skhul hominids were seen as "Neanderthaloid collaterals or cousins" to the ancestors of modern humans (p. 17). This was the only time that all of the Skhul remains have been together, a significant point in understanding their subsequent interpretations. Yet, without further comparative analysis, these remains, along with burials from nearby Qafzeh, subsequently came to be described quite differently, as "Proto-Cromagnoids" (Howell, 1959). Later excavations led to the recovery of more individuals (Vandermeersch, 1981), but an adolescent (Qafzeh IX) has since come to serve as a sort of "type" specimen for this site because it is focused upon, to the near exclusion of all other specimens, in most treatments of Qafzeh. Specimens discovered from Amud (Suzuki, 1970; Rak et al., 1994, 1996; Hovers et al., 1995) and Kebara (Bar-Yosef and Vandermeersch, 1991) were classified with the Tabun woman as Neandertals.

The question of whether and at what taxonomic level the Neandertals are distinct from modern humans has been the focus of scholarly debate and popular speculation for most of this century (Trinkaus and Shipman, 1993). Where they were defined, in Europe, the osteological differences between the two human morphs are readily apparent to even the most casual observer (Churchill, 1998; Lieberman, 1998b; Rak, 1998). Recent papers by Kimbel and Rak (1993), Lieberman (1998a), and Schwartz and Tattersall (1996) all go further and claim that European Neandertals were a separate species. This claim is not simply based on the observation that Neandertals on the whole are different from modern humans, an undisputed consensus view, but more specifically argues that they have a diagnosable set of autapomorphies. The evolution of this changing interpretation has affected the interpretation of the Levantine samples because over the years it has come to be accepted that Levantine

[1] According to Cavalli-Sforza, avoiding Neandertals in the Levant was accomplished by boating directly to Asia: he wrote that with boats "the settlement of south Asia from East Africa might have begun along its southern coast … this would have given modern humans a chance to reach Southeast Asia fairly rapidly".

Neandertal meant European Neandertal, and Levantine "early modern" meant European "early modern" (e.g., the designation of these specimens as "Proto-Cromagnoids").

Yet despite the popularity of the species interpretation, the case that the human remains from Skhul and Qafzeh are different from the Neandertals of the Levant and are "anatomically modern", or that they are in some way uniquely ancestral to the "Cro Magnons" of Europe, has never been established on comparative anatomical grounds. For instance, a recent compilation of papers reviewing the current state of knowledge about "*Neandertals and Modern Humans in **Western Asia***" (Akazawa et al., 1998 — boldface ours) does not include a single contribution dealing with the cranial evidence for separate species in the *Levant*, although the issue is addressed for Europe in several papers. Indeed, with few exceptions (e.g., Trinkaus, 1992; Schwartz and Tattersall, 1996; Arensburg and Belfer-Cohen, 1998; Stringer, 1998), this question has not been addressed for the adult Levantine cranial remains, and these exceptions reach contradictory conclusions (Fig. 1).

Understanding the evolutionary process in the Levant raises somewhat different issues than in Europe, where the Neandertals preceded the "modern" populations. It is unclear how much influence time has on the European comparison because of both evolutionary change and gene flow into the continent during the Würm Interpleniglacial (Oxygen Isotope Stage 3). In the Levant, if an emerging modern human species from Africa met Neandertals, the anatomical and behavioral differences would be maximized. One might expect competition, and surely contact, and therefore as Gould (1988) puts it, "if Neanderthals and modern humans lived in the Levant and maintained their integrity without interbreeding for 60,000 years before the great replacement in Western Europe, then the two are separate species by the primary criterion of reproductive isolation". This genetic isolation means that the two species should be at least as different as the western European "Classic Neandertals" and the succeeding European early Upper Paleolithic peoples, if not more so. We expect species competing for the same limiting resources in the same ways and not exchanging genes to accumulate genetic differences that reflect the differing adaptations. It seems quite clear that in the Levant the two groups were behaving in much the same ways (Lieberman, 1998a; Shea, 1998; Speth and Tchernov, 1998), which would elevate the potential for such competition.

Therefore, examination of the species question in the Levant seems a quite appropriate place to test the Out of Africa Theory, because, unlike in Europe, the two groups are penecontemporary, and potentially in competition. However, a review of results gathered thus far does not suggest an unambiguous conclusion. The Skhul/Qafzeh crania are not obviously modern (Frayer, 1978;
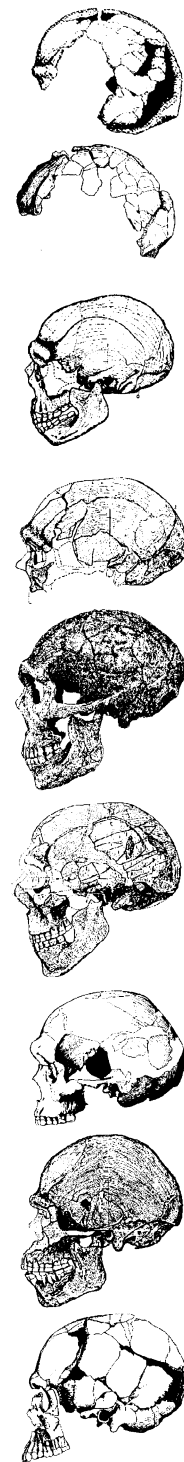

Fig. 1. Views of the most complete Levant crania. Lateral views (left) from the top are Qafzeh III and V, Tabun I, Skhul IX, Amud, Skhul IV, Qafzeh VI, Skhul V, Qafzeh IX. Facial views (right) from the top are Qafzeh III, Tabun I, Qafzeh VI, Skhul IV, Amud 1, Skhul V, and Qafzeh IX. After McCown and Keith (1939), Larsen et al. (1993), and Vandermeersch (1981).

Corruccini, 1992; Kidder et al., 1992). In fact, in spite of the new discoveries, many subsequent anatomical studies support McCown and Keith's original interpretations

Table 1
The extremes of variation at Mount Carmel, as abstracted from McCown and Keith (1939), for Skhul (Sk) and Tabun (T) specimens

Feature	Specimen(s) at the extremes	
	Paleoanthropic (i.e. Neandertal-like)	Neanthropic (i.e. modern human-like)
Cranial characteristics		
Nasal index	T I	Sk V
Nasal process of maxilla	Sk IV	Sk V
Nasal roof notched	T I, Sk IX	Sk 2, V
Narrow nasal bones	T I	Sk V
Orbit height	Sk IX	Sk V
Mastoid process	T I, Sk VII	Sk IV, V
Nuchal area breadth	Sk VI	T I, Sk V, IX
Mandibular characteristics		
Mental eminence	T I	Sk IV, V
Postcranial characteristics		
Thorax barrel-shaped	T I	Sk IV
Intercostal muscle expansion	Sk V	T I
Thickened rib cross section	T I, Sk V	Sk IV, VII
Medial ridge of ribs	Sk V	Sk IV
Elongated pubis	Sk IX	Sk IV
Scapular coracoid morphology	T I	Sk V
Clavicle morphology	T I	Sk V
Width of the forearm	T I, Sk VII	Sk V
Relative radius length	Sk V	Sk IV, T I
Curved radius shaft	T I, Sk VII	Sk IV, V
Relative size of distal radius end	T I	Sk VII
Curved ulna shaft	T I, Sk VII	Sk IV
Form of coronoid process	Sk 2, T I	Sk V
Uncinate process of the hamate	T I	Sk V
Apical tuberosity of triquetrum	Sk IV	T I
General carpal morphology	T I	Sk V
Relative femur shaft robustness	Sk V	Sk IV
Femur shaft curvature index	Sk VI	T I
Lesser trochanter expression	T I	Sk IV, V
Linea aspera and pilaster expression	T I, Sk VII	Sk IV
Midshaft rounding	T I, Sk VII	Sk V
Horizontality of tibial condyles	T I	Sk IV
Fibular shaft rounding	T I	Sk IV
Morphology of the foot	T I	Sk IV

that "paleoanthropic" (their term) features are mixed throughout the Skhul remains (Table 1). For these and other reasons, a number of researchers have come to the conclusion that the Levantine sample as a whole cannot be clearly separated into "Neanderthaloid" and "modern" sets (Simmons et al., 1991; Corruccini, 1992; Sohn and Wolpoff, 1993; Creed-Miles et al., 1996; Arensburg and Belfer-Cohen, 1998).

It is obvious that a consensus has not been reached, and the issue of whether emerging modern humans from Africa and Neandertal émigrés from Europe who encountered each other there were different species, remains unresolved. The Levantine record is unique in preserving the best evidence of penecontemporaneity and geographic overlap of Neandertals and "modern humans", and it is the one place where it *should* be

resolvable. The issue has been discussed in some detail for the case of Levantine children (Trinkaus, 1993, 1994; Arensburg, 1994; Rak et al., 1994, 1996; Creed-Miles et al., 1996; Tillier, 1998). In this paper we use phylogenetic and other clustering techniques to try to refute the null hypothesis, namely that the Late Pleistocene adult Levantine crania from Skhul, Tabun, Qafzeh, and Amud are samples from a single human species.

2. Materials and methods

2.1. Cladistic methodology

To test the hypothesis that the Levantine "Neandertals" and the Skhul/Qafzeh remains cannot be separated

into species groups, we propose beginning with a phylogenetic approach. In particular, we will examine cranial non-metrics for the samples, thereby for the most part avoiding problems of allometry and other scaling factors that result from differences in size of specimens, and differences in the magnitudes of metric traits that might be examined. Our goal is not to ascertain the best-supported phylogeny for the specimens, but rather to examine a null hypothesis that they form a single species group. Our underlying assumption in this test is that if there are two species groups, they will form distinct clusters. In making this assumption, we do *not* propose that phylogenetic clustering can be used to identify species. We are not trying to demonstrate that there are two (or more) species with this approach, but are trying to reject a null hypothesis that there is a single species group.

Fossil species recognition questions such as this are not appropriately addressed by traditional cladistic approaches because the minimal "operational taxonomic unit" (OTU) *is* the species (Hennig, 1966). This is necessary because the only way to have confidence that branches in a cladogram will not reticulate is to presume reproductive discontinuity had been established at the nodes by speciation events. Therefore, using taxa at the species level or higher, it can be logically assumed that the phylogeny can be represented by a branching pattern. In contrast, and confounding the assumptions of cladistic analysis, infra-species relationships can be reticulate and not necessarily bifurcating (Harrison, 1993). As a result, cladistic analyses presume the presence of multiple species with the initial identification of three or more OTUs (two ingroup taxa and an outgroup).

We suggest that treating individual specimens as OTUs in testing null hypotheses such as this one is a worthwhile, alternative approach to species recognition that avoids the pitfalls of traditional cladistic analysis while maintaining its advantages in evaluating hypotheses. We do not propose to use this approach to determine the exact phylogeny of the individual specimens; indeed, because at least some of them form potentially reticulating groups, they can have no phylogeny in the traditional sense. Instead, we use this approach to try and refute the hypothesis that the sample forms one single group. This task is simplified by the fact that if it can be shown that there is more than one group, it is widely appreciated that the two groups involved are Neandertals (Tabun, Amud) and early "modern" humans (Skhul, Qafzeh). Thus, we need not use phylogenetics to ascertain group membership. Rather, the cladistic analysis of individuals is used as a heuristic clustering procedure. Individuals representing two different species would be expected to occupy two different clades; and if they do not, we question whether the known information is sufficient to allow the interpretation of two species. Conspecifics are expected to form a branching pattern that would not necessarily be cladistically distinct.

The three cladistic analyses we performed used the computerized cladistic program PAUP* 4.0 (Phylogenetic Analysis Using Parsimony *and Other Methods; Swofford, 1998). Because of the limited size of the fossil data sets preserved for analysis, PAUP* was able to complete exhaustive searches for all possible trees for each analysis. Trees were evaluated using the Branch and Bound search algorithm employing the maximum parsimony optimality criterion. A 50% majority rule consensus tree was constructed from the most parsimonious trees retained in each analysis. This consensus tree depicts the groupings that appeared in at least half of the shortest trees. Finally, bootstrap analyses of these data (1000 replicates each) were undertaken to statistically evaluate the reliability of the groupings produced by the parsimony analyses.

2.2. Pairwise differences

Because we did not want to rely uniquely on a tree-based methodology to examine this question at the level of individual specimens, we also conducted a pairwise difference analysis to examine whether or not the two Levantine Neandertals were linked by a minimum number of differences in their non-metric trait comparisons. Pairwise difference analysis has been applied to DNA sequence data to investigate the closeness of relationship that a single ancient individual has to samples of living humans from different regions of the world (Krings et al., 1997). In these genetic analyses, the number of nucleotide differences between all possible pairs of individual DNA sequences are counted, and the results are presented as the frequency distribution of the number of differences. The assumptions are that each difference represents a mutation and that individuals who share fewer pairwise differences are more closely related because fewer mutations separate them. A similar assumption underlies all phenetic clustering techniques, where similarity is assumed to reflect relationship. Such procedures treat the variation in each trait under the assumption that they respond to comparable genetic bases, and consider individuals who cluster more closely to be more closely related to each other.

2.3. Sample selection and rationale

The OTUs for these analyses consisted of the most complete Levantine cranial specimens, employed to maximize both sample size and trait coverage across all regions of the skull. Amud and Tabun represent the Levantine "Neandertals", while the "moderns" include Skhul IV, V and IX, and Qafzeh III, VI and IX. The most debilitating problem in virtually all fossil studies is sample size. Like many before us, we faced the reciprocal problems of maximizing the number of traits and the number of specimens. There are so few complete

specimens that analyzing them alone would ignore key elements of variation and make the results little more than an exercise in typology. Therefore, we chose to maximize the number of specimens at the expense of maximizing their completeness.

As much as considerations of sample size allowed, we made sure that our traits accommodated all the observations reported in the literature as distinguishing *Levantine* Neandertals from the other *Levantine* crania (especially Trinkaus, 1992). Practically, though, this means we had to accept the limitations of the trade off between maximizing sample size and maximizing the features we could examine. We felt confident that we could choose the former, because it has been argued that many features from all parts of the cranial and post-cranial skeleton distinguish Neandertal from modern human species (Lieberman, 1998a, b; Rak, 1998). We could not include some obvious and recently discussed features, such as the anatomy of the anterior nasal fossa (Schwartz and Tattersall (1996), but see Franciscus (1999)), or the presence or absence of a chin, because this would make our very limited samples even smaller, since not all specimens have nasal fossae or mandibles. Moreover, it is far from clear that features such as these, said to distinguish the European Neandertals from their "early modern" successors, also distinguish the penecontemporary Neandertal and Skhul/Qafzeh samples in the Levant.

Before we attempted the cladistic treatment of the Levantine crania, we undertook two analyses involving Western European Neandertals and early Upper Paleolithic *Homo sapiens* to verify that our methodology provided an appropriate test of the null hypothesis. The first of these tested whether or not the characters used in this study could distinguish Neandertals from modern humans where these groups were first defined, in Europe. To do this we compared three European "Classic" Neandertal males (Monte Circeo, La Ferrassie, La Chapelle) to three early modern human males (Brno II, Mladec V, Predmostí III). Secondly, we wanted to determine if these features produce groupings according to sex rather than by taxon. The three European Neandertal males were compared to three female counterparts (La Quina V, Gibraltar, Krapina C). Table 2 provides a complete listing of the fossil hominids utilized in all of our analyses.

To root the phylogenetic analyses and to determine trait polarities, early Pleistocene African *Homo* (as represented by KNM-ER 3733) was employed for outgroup comparisons. This specimen was chosen because it is the earliest known complete adult cranium, and it is related equally to all of the individuals considered here. Justification for this decision was provided by Hennig's (1966) auxiliary outgroup criterion of geological character precedence, as summarized by Wiley (1981, p. 148). Plesiomorphic or apomorphic character states were therefore assigned by treating the condition in KNM-ER 3733 as plesiomorphic.

Table 2
Fossil hominid specimens employed in this study

Analysis 1: Neandertal males versus early modern human males (Fig. 2)	
Neandertals	Early modern humans
Monte Circeo	Brno II
La Ferrassie	Mladec V
La Chapelle-aux-Saints	Predmosti III

Analysis 2: Neandertal males versus Neandertal females (Fig. 3)	
Males	Females
Monte Circeo	La Quina V
La Ferrassie	Gibraltar
La Chapelle-aux-Saints	Krapina C

Analysis 3: The Levantine Neandertals versus early modern humans (Fig. 4)	
Neandertals	Early modern humans
Tabun	Skhul IV
Amud	Skhul V
	Skhul IX
	Qafzeh III
	Qafzeh VI
	Qafzeh IX

2.3.1. Non-metric cranial traits

The non-metric cranial features (Table 3) utilized in our analyses were selected in order to maximize information content and to minimize the number of missing scores in the resulting data matrix. We chose the traits that could be clearly and unambiguously scored on most or all of the Levantine specimens.

The features we used are not always the same as the traits that distinguish the European Neandertals from the Skhul/Qafzeh crania (Hublin, 1998; Rak, 1998). In part this is because the sample preservation is different (facial preservation in the Levant specimens does not allow for some key observations possible for our Europeans), and in part it is because of systematic anatomical differences between the European and Levantine Neandertals (Trinkaus, 1992; Arensburg and Belfer-Cohen, 1998; Wolpoff, 1999). Of course, it may be that differences in Europe are easier to establish because their anatomical preservation is better. In the absence of corresponding data for the Levantine specimens this notion is impossible to test, but we cannot *assume* it would be true if such data had been preserved because this would be assuming our conclusions. In any event, this fact shows that the Levantine analysis is bound to be less powerful.

The 12 traits we evaluate were selected from a larger set of possible features because this dozen, unlike the others, displayed variation in character state expression among the fossils being analyzed. Each author scored character states on casts of the fossil crania. Table 3 provides descriptions of each of the 12 characters and their plesiomorphic and apomorphic states.

Table 3
Non-metric cranial features employed in this study and their plesiomorphic and apomorphic states. In all cases KNM-ER 3733 is used to define the plesiomorphic condition

Character	Plesiomorphic state	Apomorphic state
(1) Suprainiac fossa	Absent	Present
(2) Maximum cranial breadth	Low, at or about supramastoid crest	High, in the parietal region
(3) Posterior parietal form	Flattened sagittally above lambda	Rounded sagittally above lambda
(4) Digastric sulcus form	Narrow and relatively deeply incised	Broad and relatively shallow
(5) Occipitomastoid crest size	As large, or larger, than mastoid process	Much smaller than mastoid process
(6) Anterior glenoid slope	Shallow, $\leqslant 45°$	Steep, $> 45°$
(7) Postglenoid tubercle	Present	Absent
(8) Frontal–sagittal keel	Present	Absent
(9) Lateral frontal boss	Absent	Present
(10) Glabellar bulge	Absent	Present
(11) Central occipital torus form	Projecting, lateral portion relatively flat	Depressed, lateral portion relatively thick
(12) Supraorbital torus form	Uniformly thick	Thins laterally

Table 4
Data matrix employed by PAUP analyses.[a] Details of the features are described in Table 3

Fossil hominids	Cranial non-metric features[b]											
	1	2	3	4	5	6	7	8	9	10	11	12
KNM-ER 3733 (outgroup)	0	0	0	0	0	0	0	0	0	0	0	0
Brno II	1	1	0	0	1		1	1	1	1	0	1
Mladec	0	1	0	0	1	1	0	0	1	0	0	1
Predmostí III	1	0	0	1	1	1	1	0	1	0	0	1
Monte Circeo	1	0	0	1	0	0	0	1	0	1	1	0
La Ferrassie	1	0	1	0	0	0	0	1	0	1	1	1
La Chapelle-aux-Saints	1	0	0	0	0	0	1	1	0	1	1	1
La Quina V	1	0	1	0	1	0	0	0	0	1	1	0
Gibraltar	1	0	0	0	0	0	1	1	0	1	1	0
Krapina C	1	0	0	1	0	1	0	1	0	0	1	1
Tabun	1	1	1	0	0	0	0	1	1	0	1	0
Amud	1	0	0	0	1	0	0	0	1	1	1	1
Skhul IV	0	0	1	1	0	1	1	1	1	0	0	0
Skhul V	1	1	0	1	1	1	1	1	1	1	1	1
Skhul IX	0	0	1	1	0						0	1
Qafzeh III	0	1	1	0	0			1	1	0	0	1
Qafzeh VI	1	0	0	1	1	1	1	1	0	1	0	0
Qafzeh IX	0	1	1	0	1	1	0	1	1	1	1	1

[a] 0 = plesiomorphic, 1 = apomorphic, blank = missing.
[b] See Table 3 for listing and descriptions of traits by number.

Table 4 provides the data matrix for the 17 specimens (including the outgroup specimen KNM-ER 3733) utilized in this study.

We used these features in a phylogenetic analysis to attempt refutation of the null hypothesis. We accepted a 95 percentile criterion — if 5% or more of the most highly supported trees based on individuals clustered Tabun and Amud together, to the exclusion of all the Skhul and Qafzeh specimens, we accepted the null hypothesis as rejected.

We also use pairwise analysis here, to examine the relationship of the Levantine Neandertals to each other and to the Skhul/Qafzeh crania, based on the 12 non-metric traits described in Table 3. Our non-metric traits were scored as presence or absence, so that the differences could be validly combined without weighing one more than another. The chance of a Type I error based on scaling is high with this test only if the Neandertal crania are more similar in size to each other than they are to Skhul/Qafzeh crania, and this is manifestly *not* the case.
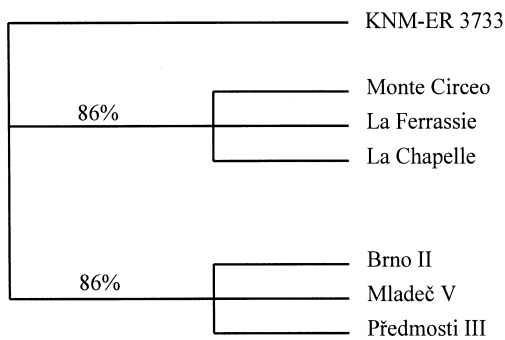
Fig. 2. Analysis 1: Neandertal males versus early modern European males. The 50% majority rule consensus tree of the seven most parsimonious cladograms (tree length = 19) generated by PAUP*, demonstrating that "Classic" western European Neandertals can be cladistically distinguished from succeeding Early Upper Paleolithic *Homo sapiens* using our approach. Six of the seven (86%) shortest trees depicted Neandertals on a clade distinct from that occupied by the early modern humans. The characters and their states are given in Table 3.

3. Results

3.1. Analysis 1: Does it work? Could our traits and procedure distinguish European Neandertals from early modern Europeans?

To start, PAUP* was applied to an analysis of the western European male crania: three "Classic Neandertals" and three males representing early Upper Paleolithic *Homo sapiens* (see Table 2 for a listing of the specimens employed). PAUP* evaluated 945 trees, ranging in length from 19 to 29 steps. Six of the seven (85.7%) most parsimonious cladograms (tree length = 19) displayed a Neandertal clade distinct from an Upper Paleolithic human clade. Fig. 2, the 50% majority rule consensus tree, depicts this distinction. The bootstrap analysis provides qualified support for the parsi-

mony analysis in that the Neandertal (60.3%) and Upper Paleolithic human (58.9%) clades are the most frequent groupings replicated. It appears that our cladistic data set accurately distinguishes Neandertal from early modern human morphology. Table 5 provides summary statistics for the three cladistic analyses.

3.2. Analysis 2: Sexual dimorphism? European Neandertal males versus females

Next, six Neandertal crania were evaluated: three western European females and three males (Table 2). Again, nearly 1000 trees were found in PAUP*'s exhaustive search, ranging in length from 14 to 17 steps. Of the 21 shortest trees (tree length = 14), none displayed a "male Neandertal" grouping separate from a female grouping. Of the three groupings common to at least half of the shortest trees preserved by the 50% majority rule consensus tree (Fig. 3), none correspond to a sexual division of the sample. This result is mirrored by the bootstrap analysis in which a male/female dichotomy failed to appear. The potential influence of sex on the distribution of these characters in a mixed-sex cranial sample can be dismissed because our set of traits does not produce groupings according to sex.

The results from the first two analyses suggest the following: (1) the features employed can, and consistently do, distinguish "modern human" from "Neandertal" morphology in Europe and (2) these characters are not simply discriminating by sex. Therefore, if Neandertals and early moderns were present as separate entities in the Levant as they were in Europe, an analysis of this sort, *using these features*, should be able to consistently separate the two clades even though fewer characteristics are preserved in the Levantine sample and we have reason to believe that the Levantine data are less well structured for this reason.

Table 5
Summary tree measures for cladistic analyses

Analysis	Number of trees		Tree lengths		Indices[a]		
	Evaluated	Retained	Minimum	Maximum	CI[b]	RI[c]	RC[d]
1: Neandertals versus early modern humans	945	7	19	29	0.6316	0.5882	0.3715
2: Neandertal males versus females	945	21	14	17	0.7143	0.4286	0.3061
3: Levant Neandertals versus Levant early modern humans	135,135	17	26	42	0.4615	0.5333	0.2642

[a] Indices are listed for the most parsimonious trees retained (minimum tree lengths). All definitions from Wiley et al. (1991).
[b] CI (consistency index) — the ratio of the minimum amount of character state transformations a tree may display versus the actual amount of character state transformations a tree does display.
[c] RI (retention index) — the fraction of apparent synapomorphy to actual synapomorphy.
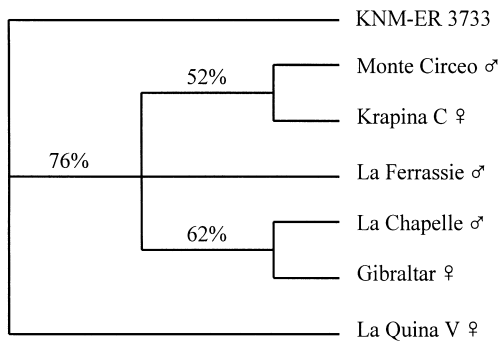[d] RC (rescaled consistency index) — the product of the CI and the RI.

Fig. 3. Analysis 2: Neandertal males (Mt. Circeo, La Chapelle, La Ferrassie) versus Neandertal females (Gibraltar, La Quina V, Krapina C). The 50% majority rule consensus tree of the 21 most parsimonious cladograms (length = 14) generated by PAUP*, demonstrating that sex had no influence on the cladistic groupings of the European Neandertals. None of the 21 shortest trees displayed a male Neandertal clade separate from a female branch. The characters and their states are given in Table 3.

Fig. 4. Analysis 3: Levantine "Neandertals" versus Levantine "early modern humans". The 50% majority rule consensus tree for the 17 most parsimonious cladograms (tree length = 26) generated by PAUP*. Tabun and Amud (the putative Neandertals) are not cladistically distinct from the supposed "early moderns" from Skhul/Qafzeh. None of the 17 shortest trees displayed a Tabun/Amud clade separate from that of Skhul/Qafzeh. The characters and their states are given in Table 3.

3.3. Analysis 3: The Levantine hominids

Our Levantine cranial sample included the eight most complete specimens: Tabun and Amud, typically regarded as "Neandertals", and the supposed "early modern humans" from Skhul and Qafzeh (Table 1). Over 135,000 trees were evaluated by PAUP* in this analysis, ranging in length from 26 to 42 steps. Of the 17 most parsimonious trees (length = 26) *not one* revealed a Neandertal clade of Tabun and Amud distinct from the early moderns from Skhul and Qafzeh. However, it should be noted that the Consistency Index (CI) for these cladograms was a relatively low 0.462. The 50% majority rule consensus tree (Fig. 4) preserves three groupings that were common to at least half of the 17 shortest trees. In 16 of these 17 trees (94.1%) a clade including Amud, Skhul V, Qafzeh VI and Qafzeh IX was identified to the exclusion of all others. The next most frequent grouping of Skhul V and Qafzeh VI appeared in 13 trees (76.5%) and the only other clade that appeared more than 50% of the time was Amud, Skhul V and Qafzeh VI in 11 trees (64.7%). The bootstrap analysis again supported the parsimony analysis, however this support is tempered by the fact that none of the bootstrapped groupings appeared in > 40% of the replicates. Amud and Tabun appear in varying frequencies with the Skhul and Qafzeh specimens [e.g. (Amud, Skhul V, Qafzeh VI, Qafzeh IX: 27.7%), (Amud, Skhul V, Qafzeh VI: 26.4%), and (Tabun, all Skhul and all Qafzeh: 21.5%)]. In contrast, the unique Skhul/Qafzeh clade was reproduced in the bootstrap analysis in only 11.2% of the replicates and the Amud/Tabun clade appeared in only 6.9%.

Analyses 1 and 2 described above show that the results of Analysis 3 cannot be due to a possible sex difference of the two Neandertals, nor to the inability of the cladistic
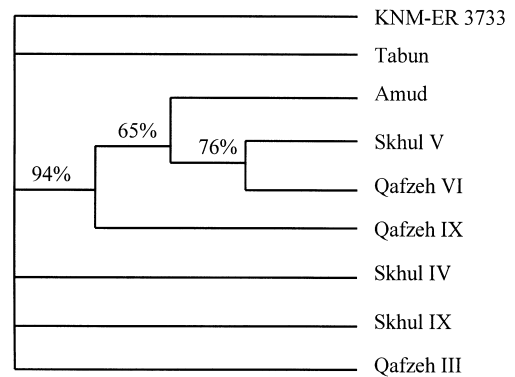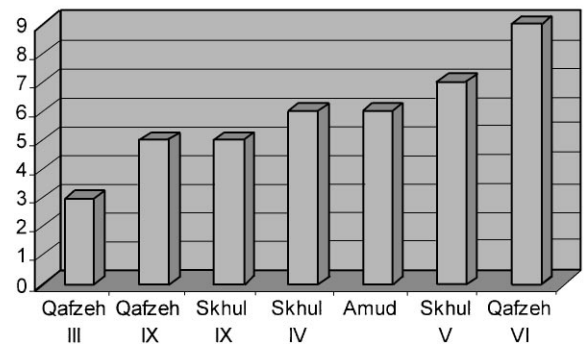

Fig. 5. Analysis of pairwise differences between Tabun and the other Levantine crania.

program to distinguish Neandertal from modern human morphology.

3.4. Analysis 4: Pairwise differences

Tabun was compared with the other Levantine crania in the pairwise difference analysis shown in Fig. 5, based on the non-metric data in Table 1. The mean difference of Tabun from the Skhul/Qafzeh crania was 5.8, which does not differ significantly from the six differences between Tabun and Amud. Only two of the six Skhul/Qafzeh crania differ more from Tabun than Amud does.

4. Discussion and conclusions

If Neandertals and early modern humans (in the Levant) were behaviorally more similar to each other

than they are to recent modern humans, should we place them in the same taxon as some researchers argue? The answer is clearly no. " … Morphological characteristics, not archaeological residues, are the … most reliable source of information to assess their systematic relationships. Neandertals and early modern humans most likely belong to separate taxa because *each have a unique set of derived characters (autapomorphies)*." (Lieberman, 1998a, p. 272, italics ours)

It has been our goal to search for such a unique set of derived characters distinguishing part of the Levantine sample, because this would be a clear refutation of the null hypothesis. Such a unique set of derived features would establish grounds for arguing that the populations with presumably different geographic origins that encountered each other in the Levant were different human species, even though they could not be meaningfully distinguished behaviorally. In this search, we maximized the Levantine hominid sample size to allow our analysis to account for the variation in the sample, but nevertheless were able to identify 12 non-metric features that reflect variation in the areas where we expect such a distinction to be visible. We found that these 12 features cladistically distinguish European Neandertal cranial morphology from that of early Upper Paleolithic Europeans, and that this distinction reflects variation from sources other than sexual dimorphism. Some researchers may interpret the results of our Analysis 1, the European test, as ancillary support for the hypothesis that European Neandertals were specifically distinct from the early modern human populations that succeeded them in Europe. This is not the question addressed here, and our study would have a rather different design if we were to address a null hypothesis in Europe. The issue is different because the distinctions between the European Neandertals and early moderns may involve time as well as taxonomic diversity, and because of the potential for variation to be controlled by the evolutionary process, its pattern must be examined differently. Evolutionary changes spanning the millennia connecting the earlier Neandertals to the later modern humans, as well as gene flow into Europe during Upper Pleistocene interstadials, may account for the variation reflected in our analysis. Differences between the Levantine samples cannot be interpreted this way.

When PAUP* was applied to the Levantine crania, no phylogenetic distinctions were revealed between the cranial morphologies of Tabun and Amud from those of Skhul and Qafzeh. The null hypothesis could not be refuted because neither the Levantine "Neandertals" nor the "early moderns" display a unique set of derived characters. However, we acknowledge that the limited size of our dataset prevented us from obtaining statistical support (from bootstrapping) for our conclusions produced by the parsimony analyses. Independent of the branching analyses, our results are corroborated by the

pairwise difference study, which shows that Amud differs from the other putative "Neandertal" from Tabun more so than two-thirds of the "modern humans" from Skhul and Qafzeh.

In drawing this conclusion, we differ from Trinkaus (1992), who is the only author to specifically address differences in the crania of the two Levantine groups. He has proposed four cranial traits to separate them: (1) vault shape, and the morphologies of (2) the occipitomastoid, (3) the occipital torus and (4) the supraorbital torus. Trinkaus' "neurocranial vault shape … in *norma occipitalis*" (Feature 2 in this study) is plesiomorphic for Amud, whose maximum cranial breadth is relatively low on the cranium, while Tabun displays the derived, "modern" condition of maximum breadth in the parietal region. The "occipitomastoid morphology" (Features 5 and 11) is again variably expressed in the two Levant "Neandertals": the occipitomastoid crest is large, a plesiomorphy in Tabun, while Amud's lack of development in this region is derived in the modern human direction. Both Tabun and Amud are derived in their flattened central occipital torus, while Qafzeh III, Skhul IV, and IX display the plesiomorphic condition of a centrally projecting torus. The "shape of the supraorbital torus" (Feature 12) is uniformly thick in Tabun and Skhul IV, the plesiomorphic condition, while Amud, Qafzeh III and IX, Skhul V and IX have supraorbital tori that thin laterally. In sum, we do not agree that the four features that Trinkaus proposed actually do distinguish the groups with any consistency.

We are aware that the simple demonstration that we cannot identify a "Neandertal clade" formed by Tabun and Amud will probably not lay the Out of Africa issue to rest. As both Trinkaus (1990) and Harrison (1993) have made clear, shared polymorphisms can confound cladistic analyses of closely related taxa. Therefore, it may not be surprising that the Skhul/Qafzeh hominids share some "Neandertal-like" (= derived) features with Tabun and Amud, even if the two groups represent sister-species. Inspection of the 50% majority rule consensus cladogram (Fig. 4) reveals that the Skhul and Qafzeh crania, long perceived to be essentially "modern", run the gamut from very plesiomorphic (Skhul IV, IX, Qafzeh III) to quite derived (Skhul V, Qafzeh VI), paralleling Corruccini's (1992) phenetic analysis. We found that the oft-cited "Neandertal autapomorphies" are (1) not monolithic within the Levant Neandertals and (2) variably present in the "early moderns" from Skhul and Qafzeh. For example, Skhul V possesses a suprainiac fossa, a feature said to be uniquely derived in the Neandertal clade (Hublin, 1998; Lieberman, 1998a). For that matter, it is far from clear that the *European* Neandertals have a diagnosable set of autapomorphies (Frayer, 1993; Smith, 1994; Wolpoff, 1994, 1999; Wolpoff and Caspari, 1996; Franciscus, 1999).

Nevertheless, the persistent claims for two species in the Levant are cladistically based (e.g., Tattersall, 1986, 1996; Rak, 1993) and would predict that a comprehensive analysis of cranio-facial morphology should reveal a "Neandertal" branch distinct from those representing *H. sapiens*. This is demonstrably not the case. It may be that it is not the case because the fossils at hand are simply not sufficient to adequately test the null hypothesis using a phylogenetic approach. Perhaps so, but if this is the most acceptable explanation for why it is not the case, the null hypothesis should not be rejected. This would leave scant grounds for accepting the Out of Africa model unless it was interpreted differently, not as a theory of species replacement, but to mean that modern characteristics appeared first in Africa and as populations with them spread and expanded their range, they mixed with other human populations they encountered. Such a theory would account for the dissemination of features under selection because of their advantages (Dobzhansky, 1944), especially if Africa was more heavily populated than other regions (Relethford, 1999). However, this would no longer be Out of Africa, but a statement of Multiregional Evolution (Relethford, 1995, 1998).

The geographic position of the Levant, in association with Late Pleistocene climatic oscillations, may provide the best opportunity for understanding the origins of morphological diversity among these hominids. Today, the Levant serves as a crossroads to three continents: Europe, Africa and Asia, and there is no compelling reason to preclude this role to the region during the latter part of the Pleistocene (Bar-Yosef, 1992, 1998). Intensifying European glaciation and North African desertification may have led to periodic pulses of population movement into the Levant (cf. Simmons and Smith, 1991; Bar-Yosef, 1992) resulting in increased opportunities for gene flow between Euro-African populations and the peoples of western Asia. Here we differ from Bar-Yosef's assessment that one such pulse is sufficient to explain the details of the fossil remains, whether or not it turns out that all of the Levantine Neandertals are later than the "early moderns", as he believes. In fact there is no reason to expect that a significant influx of European (or other) populations only happened once, since the climatic conditions influencing population movements and human range expansions and contractions were multiple and cyclic throughout the Pleistocene.

Simmons (1994) proposes that to examine the hybridization issue, we treat the Levant as a contact zone between Eurasian populations and emerging Africans at the beginning of the late Pleistocene, as its geographic position would suggest (but see Marks, 1992). In such a zone of contact, we might expect species-specific characteristics to increase with time if the contact is prolonged and between different species. But if prolonged contact is between populations of the same species, per-

haps with different geographic origins, we cannot expect that the ancestral types "will continue to crystallize out of a mixed population", as Dobzhansky noted. Simmons contends, and we agree, that the Levantine sequence does not appear to reflect contact between different species. The diversity of form among the Skhul/Qafzeh hominids suggests that prolonged mixture with Neandertals had its effect on these people, indicating that Neandertals "did contribute in a quantitatively significant manner to the phenotype, and hence genetic variability, of modern human populations" (Simmons, 1994, p. 219).

Corroborating the previous research of Arensburg and Belfer-Cohen (1998), Corruccini (1992) and Kidder et al. (1992), our study suggests that the humans who occupied the Amud, Qafzeh and Mount Carmel caves were members of a single species whose variation is best perceived as analogous to that common between extant, indigenous populations of neighboring continents. When human groups come into contact, they may merge or fight, but they invariably exchange genes and ideas as well. We can see this uniformitarian principle applied in the past, in this special area of the world where circumstances of environment and ecology assured that human contact was continuous as long as there was human occupation.

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